https://doi.org/10.5194/egusphere-2026-5424
Preprint. Discussion started: 16 September 2026

Comparing estimates of gross primary production in a mature Norway spruce plantation in hemiboreal Sweden

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Abstract. Forest plantations can sequester large amounts of carbon dioxide from the atmosphere while producing commercial wood products. Quantification of carbon fluxes usually depends on the eddy covariance (EC) method, which may be biased, especially in the presence of a dense canopy. We aimed to test estimates of canopy photosynthesis, or gross primary production (GPP), derived from EC against an independent method based on transpiration (xylem sap-flux) and isotopic (tree ring $\delta^{13}C$) estimates of photosynthetic water-use efficiency. The addition of tree-ring $\delta^{13}C$ to existing sap-flux data made it possible to infer GPP in the past, including the drought year of 2018 and the years surrounding it. Previously published EC based estimates at our research site, the Central Forest at Skogaryd Research Catchment in south-western Sweden, had been unable to detect a response of annual GPP to the 2018 drought. A closer look at the daily EC data revealed a decrease of about 13% over the drought period. However, using the sap-flux and isotopes, we found a decrease in GPP of 31%, which continued for several weeks after the drought. The loss in GPP occurred primarily because water stress reduced sap flux and it occurred despite an increase in water-use efficiency. Stem biomass growth decreased in 2018, but the ratio of stem biomass growth to GPP (17%) was within the range of published values. The discrepancies highlight method differences during the severe drought and during the spring of some years, but the long periods of agreement tend to confirm the accuracy of both methods over most of the study period.

1 Introduction

Forests are a key compartment of the global carbon (C) cycle and play an important role for climate mitigation, as they remove large amounts of carbon dioxide (CO_2) from the atmosphere and store C in biomass and soils (IPCC, 2018), which is often termed the terrestrial C sink. It has been estimated by bottom-up scaling that forests worldwide contribute to this terrestrial C sink and might be responsible for the largest share of it (Pan et al., 2011, 2024). Northern (boreal) forests are responsible for about 20% of the total terrestrial C sink (Pan et al., 2011, 2024).

Those bottom-up estimates usually rely on stand level measurements of the net ecosystem production (NEP) measured using the eddy covariance (EC) methodology. Net ecosystem production, also expressed as negative NEE (Net Ecosystem Exchange), is the balance of two opposing fluxes: gross primary production (GPP) and ecosystem respiration (Reco). Eddy covariance measures NEP, but it can be used to infer GPP and Reco (Baldocchi, 2003; Campioli et al., 2016). However, there are several assumptions required for accuracy. First, EC measurements are best applicable on flat terrain with homogeneous canopies and require large areas with homogeneous conditions, i.e. the "footprint," the area measured around the EC device. Hence, the EC method is usually not applicable to plot-size trials. Moreover, the GPP inferences from EC data rely either on the assumption that night-time respiration represents daytime respiration (the nighttime method; Reichstein et al, 2005; Campioli et al., 2016) or that simultaneous fitting to light and temperature (the daytime method) attributes the correct GPP to light intensity (Lasslop et al., 2010).

Forests are especially challenging for the EC method as their elevated canopy and divergence in stratification partially decouple the air masses below and above the canopy (Thomas et al., 2013). This decoupling limits the ability of the below-

https://doi.org/10.5194/egusphere-2026-5424
Preprint. Discussion started: 16 September 2026

canopy emissions, such as those from ground vegetation and the soil, to reach the measurement equipment located above the canopy, creating uncertainty regarding whether the GPP estimate truly represents the entire stand (Etzold et al., 2010; Jocher et al., 2017). Decoupling might be especially problematic in tall, dense spruce plantations such as those measured here.

An alternative method to estimate GPP is based on well-established physiological tools and principles (Gessler et al., 2009; Hu et al., 2010; Klein et al., 2016; Vernay et al., 2020, 2024). It relies on water-use efficiency (WUE), the exchange ratio of CO_2 for water vapor during photosynthesis, and measurements of sap flow, which provide a daily estimate of transpirational water losses that occur as trees conduct photosynthesis. In this method, both sap flow and WUE are measured on individual trees. Therefore, the resulting per-tree GPP estimates must be scaled up to the stand level for comparison to EC.

One measure of WUE, the intrinsic water-use efficiency (iWUE) can be estimated from the stable carbon isotope ratios ($\delta^{13}C$) of plant tissue (Farquhar & Richards, 1984). Several previous studies have estimated $\delta^{13}C$ from phloem contents, which have the advantages of integrating over the whole canopy and being replaced every few days, providing a description of gas-exchange dynamics (Schiestl-Aalto et al., 2021). However, phloem samples must be collected at regular intervals in the field. Here we wished to explore the alternative use of $\delta^{13}C$ in the annual rings of trees (Klein et al., 2016) rather than phloem, because annual rings can be collected and precisely tied to annual production long after the wood was produced.

Our specific aims were to:

i. Compare estimates of photosynthetic water-use efficiency and sap flux between the drought of 2018 and the same dates in the years surrounding it;
ii. Compare estimates of GPP via water-use efficiency and sap flux vs. eddy covariance over several years; and
iii. Estimate partitioning of GPP to stem production in this rapidly growing spruce plantation.

2 Methods

2.1 Central Forest – site description

The Central Forest at Skogaryd Research Catchment is an 8.7 ha forest stand of first-generation Norway spruce (*Picea abies* (L.) Karst.), planted in the early 1960's on land previously used for agriculture. The soil at the site is a drained, nutrient rich Umbrisol, with a depth of 60 – 80 cm of sandy loam overlying a water-impermeable clay layer (the "mineral" site in Aurangojeb et al., 2017).

In summer and autumn 2021 tree diameter and height were measured for estimation of biomass. Within the stand, 7 circular plots with a radius of 15 m were set up and the center of each was marked. The plots were distributed within the 85 % daytime eddy covariance footprint and Plot 2, where sap-flux and $\delta^{13}C$ were measured, was located within the 55% footprint. The position of each tree in relation to the plot centre was measured using a Haglöf DP Postex system (Haglöf Sweden AB, Langsele, Sweden). With a connected digital caliper, all trees with a diameter at breast height (DBH) larger than 10 cm were measured, but the even-age plantation generally lacked smaller trees. From each living tree within the plots the DBH was measured twice at 90° angle. Tree height was measured with a Haglöf Vertex (Haglöf Sweden AB, Langsele, Sweden) from as many spruce trees as possible within the plots. A height-diameter curve (Fig. 1) was then used to calculate height for all spruce trees to be used for determination of biomass.

Tree biomass was calculated based on DBH and tree height (for spruce only) using allometric equations. First the biomass was calculated separately for the stems and branches, including foliage, as well as belowground biomass using equations provided by Marklund (1988) and Petterson and Ståhl (2006), respectively. The biomass of the components was then summarized to provide total biomass per tree. Seven percent of the trees in the stand were birch. For these the birch equations were used, based only on DBH.

Increment cores were taken from 16 spruce trees on the plot and ring widths were determined for the years with sap flux measurements (2015-2019). The tree ring widths were used to estimate biomass growth rates for the stems based on annual

https://doi.org/10.5194/egusphere-2026-5424
Preprint. Discussion started: 16 September 2026

changes in the predictions of the Marklund (1988) functions. This approach is suitable because the stems did not lose biomass during the study period; any new production was accumulated, simplifying the C accounting.

2.2 Climatic parameters

Air temperature, air pressure, relative humidity and incoming short-wave radiation were measured every half-hour above the forest canopy, while precipitation was measured at the ICOS station Mycklemossen, about 1.1 km from the site (data available at https://data.fieldsites.se/portal). Vapor pressure deficit (VPD in kPa) was calculated according to Murray (1967) based on measured air temperature (Ta in °C) and relative humidity (Rh in %) at the top of the canopy:

$$VPD = 0.61078 \times e^{\left(\frac{17.27 \times Ta}{Ta+273.16-35.86}\right)} \times \left(1 - \frac{Rh}{100}\right) \quad (1)$$

Daily average of daytime VPD was calculated (VPD_D), where daytime was defined by incoming short-wave radiation > 0 W/m^2.

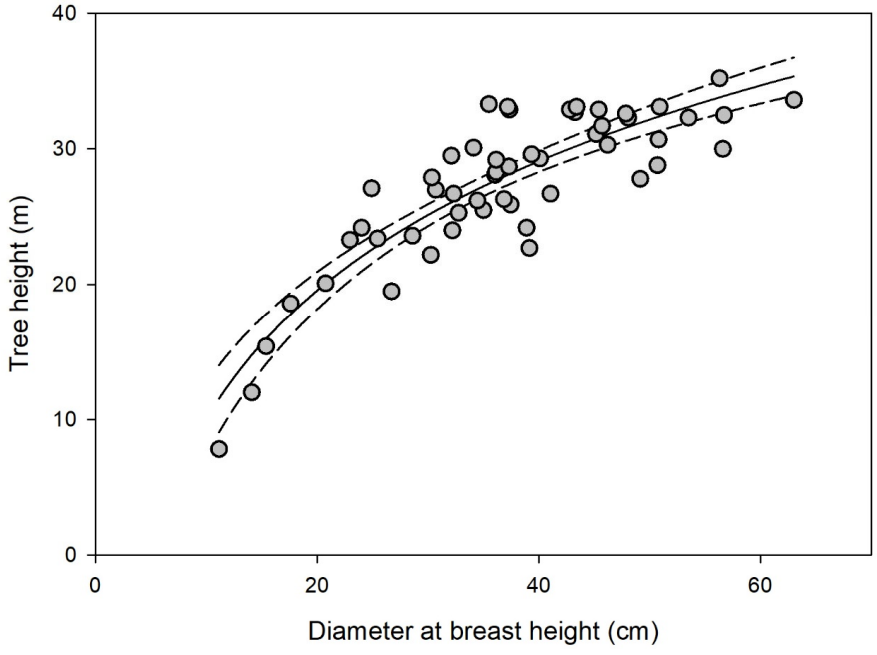

Fig. 1. Relationship between tree height and diameter at breast height for Norway spruce trees at the Central Forest, Skogaryd Research Site, including regression line and 95% confidence intervals (R^2 = 0.78).

2.3 Sap-flow measurements

Sap-flow was measured using EMS 81 (Environmental Measuring Systems, Brno, Czech Republic) devices based on the principle of trunk heat balance (Čermák et al., 2004). The devices were installed in twelve trees ranging in diameter from 32.1 to 53.5 cm in the fall of 2014, representing the size distribution of the stand. The sensors were placed in needles, which were fitted into four stainless-steel plates driven into the sapwood. The sensors were moved laterally around the stem in the spring 2017 to escape long-term wounding and to ensure that the conductive outer sapwood was included in the measured stem volume. Because the startup dates varied among growing seasons, we selected a common period (Apr 1 to Oct 31) for comparisons among years. When there were gaps within this period (9%), we filled them using data from the same dates in the gap-free year 2016. In addition to being gap-free, 2016 had the advantage of being near the middle of the whole measurement period. One tree had a needle broken in 2017; it was dropped from the sums for the whole of 2017 and the years

https://doi.org/10.5194/egusphere-2026-5424
Preprint. Discussion started: 16 September 2026

afterward. There was no sign of reductions in sapflow during the years when the needles were left in place except that the sapflow rates were unusually high in spring of 2015, the first spring after the 2014 needle installation, which was also the wettest year of the five.

2.4 Tree ring isotopes

In spring 2022 two tree cores each were taken from all sap-flow trees. From these new cores, annual rings were sliced with a razor. The entire annual ring of the years with sap-flow measurements was sliced into thin strips for rapid combustion. It was packed into a tin capsule and the ^{13}C was analyzed on a 20-22 isotope ratio mass spectrometer interfaced with a GSL elemental analyzer (Sercon Ltd., Crewe, UK). From the isotope value for the whole tree ring we calculated the isotope value of cellulose by adding an offset of 1.365‰ (Helle et al., 2022).

2.5 Eddy covariance measurements

The EC data have partially been published previously (Lindroth et al., 2020; Junttila et al., 2023), but we here present for the first time the complete time series 2015-2020 for NEP and GPP. The measurements were made at 33 m, well above the mean tree height of 27 m (Table 1), using an EC 155 gas analyser and a CSAT3A sonic anemometer, both from Campbell Scientific (Campbell Scientific, Logan, Utah, USA). The post-processing of the EC data was made with the REddyProc online tool (Wutzler et al., 2018). The data were u* filtered according to Papale et al. (2006), gap-filled and GPP was estimated by the nighttime method (Reichstein et al., 2005). The EC flux footprint was estimated with a two-dimensional footprint model (Kljun et al., 2015).

2.6 Calculations

The GPP of individual trees was estimated as the product of iWUE and stomatal conductance (g_s). The g_s for CO_2 was calculated according to:

$$g_s = \frac{Tr \times p_a}{1.6 \times \mathrm{VPDD}} \quad (2)$$

with p_a atmospheric pressure (kPa), Tr transpiration and daytime vapour pressure deficit (VPD_D) calculated as above. For Tr we used the daily sap flux measured per tree and growing season [mol H_2O $tree^{-1}$ d^{-1}]. We filtered values when VPD_D was less than 0.02 kPa because division by small values yielded large errors and because we assume that transpiration rates (and photosynthetic rates) were negligible under these conditions (Vernay et al., 2020; Stojanović et al., 2024). Even after filtration, the conductance estimates were variable at the low end of the VPD range. Therefore, we smoothed the data by estimating averages over a nine-day period, bracketing the date of interest. These averages included the zeroes that resulted when the VPD threshold was not reached.

The iWUE [µmol CO_2 mol^{-1} H_2O] was calculated based on the $\delta^{13}C$ of the tree rings (Klein et al., 2016):

$$iWUE = \frac{c_a}{r} \times \frac{b - \Delta - pr \times \frac{\Gamma^*}{c_a}}{b - a + (b - a_m) \times \frac{g_s}{r \times g_i}} \quad (3)$$

Where *Ca* is the atmospheric CO_2 concentration (ppm), r is the ratio of the diffusivities of CO_2 and water vapor in air (1.6), a, a_m, b and pr are the leaf-level ^{13}C fractionation during CO_2 diffusion through the stomata (4.4‰), during CO_2 diffusion through liquid phase (1.8‰), during carboxylation (29‰), and during photorespiration (16.2‰), respectively (Vernay et al., 2020). We used Δ as the observed tree discrimination against ^{13}C during gas-exchange, Γ^* is the temperature-dependent CO_2 compensation point of *ca.* 45 ppm (Maseyk et al., 2008), and g_s/g_i is the ratio between stomatal and internal conductance to CO_2 (0.68 for *Picea abies* according to Vernay et al. (2024)).

Isotopic discrimination (Δ) was estimated to adjust the measured $\delta^{13}C$ of the tree rings for $\delta^{13}C$ of the atmosphere ($\delta^{13}C_{atm}$) in the year of sampling (Farquhar & Richards, 1984). Atmospheric data were measured at the Pallas-Sammaltunturi site in

https://doi.org/10.5194/egusphere-2026-5424
Preprint. Discussion started: 16 September 2026

Finland (https://gml.noaa.gov/aftp/data/trace_gases/co2/flask/surface/txt/co2_pal_surface-flask_1_ccgg_month.txt). The value of Δ was estimated as follows, with all $\delta^{13}C$ values expressed in units of ‰:

$$\Delta = \frac{\delta^{13}Catm - \delta^{13}C}{1+\frac{\delta^{13}C}{1000}} \quad (4)$$

Finally, the GPP [g CO_2 $tree^{-1}$ yr^{-1}] was calculated as:

$$GPP = iWUE \; x \; g_s \; x \; \frac{M}{10^6} \quad (5)$$

With M the molar mass of CO_2.

We compared the per-tree GPP estimates derived from sap-flux and stable isotopes to those derived from EC by averaging the per-tree daily values and multiplying by the number of trees per hectare. This simple scaling was possible because the trees were planted with equal spacing in a uniform plantation and because the size distribution of sap-flux trees was representative of the size distribution of the whole stand.

We used the gap-filled daily photosynthesis data to compare the methods among years. We focused on the period between Apr 1 and Oct 31 because the sapflow data were most complete between these dates and because most (92%, according to EC) of the annual photosynthesis occurs between these dates.

3 Results

3.1 Biomass plots

The stand is described in Table 1. The trees on plot 2, where the sap-flux was measured, averaged 38.2 (± 9.5) cm diameter, slightly larger than the stand average. The sap-flux trees were slightly larger still, at 40.7 (± 10.1) cm, but this difference was statistically not significant (t-Test; P=0.58). The non-significant t-test and the similar standard deviations support the notion that the sap flux trees are representative of the stand as a whole. Diameter distributions of the spruce trees and the non-spruce trees are shown in Figs. S1 and S2, respectively. The relationship between tree height and diameter is presented in Fig. 1.

Table 1. Descriptive statistics for the Norway spruce plantation Central forest, at Skogaryd Research Site. If not stated otherwise, the measurements were made in 2020 and 2021.

Parameter (units)	Mean	Std Dev.	N
Density (trees ha^{-1})	416	124	7 plots
Percentage spruce (% of biomass)	95	4	7 plots
Diameter at breast height (cm)	37.4	10.4	206 trees
Diameter of sapflux trees 2018 (cm)	40.7	8.2	12 trees
Height (m)	27.4	5.6	53 trees
Basal area (m^2 ha^{-1})	49.3	14.5	7 plots
Total biomass (kg C m^{-2})	19.0	5.6	7 plots
Diameter growth 2015-2019 (mm y^{-1})	3.16	1.54	16 trees
Stemwood production (g C m^{-2} yr^{-1})	237	129	7 trees
Stemwood production (g C $tree^{-1}$ yr^{-1})	5960	3090	7 trees

3.2 Sap-flux

Mean sap-flux varied by date. As an example, we present the last year of the study, 2019 (Fig. 2), which had measurements every day during the entire year. Sap-flux showed a clear increase starting around day 70, followed by a series of stops and

https://doi.org/10.5194/egusphere-2026-5424
Preprint. Discussion started: 16 September 2026

starts until about day 170, at which point it stabilized around 60 L tree^{-1} day^{-1} until about day 210, and then began to fall again as winter approached (Fig. 2). The average daily sap-flux was similar among years, except in 2016 which had lower fluxes (Fig. 3).

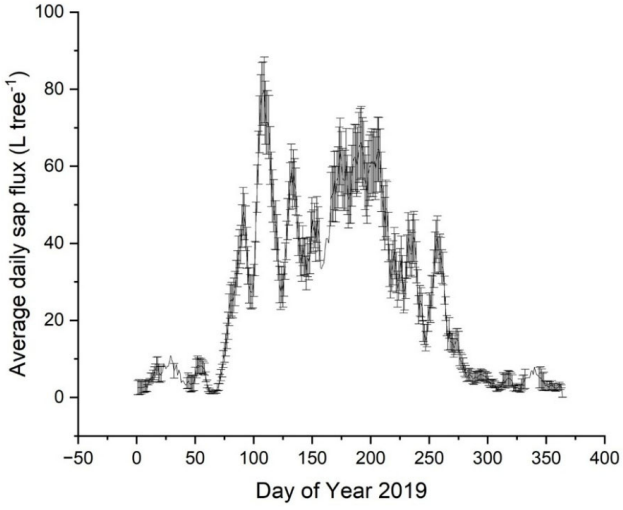

Fig. 2. Daily sap-flux in 2019, the year of most complete data coverage. The data are presented as an example to show the seasonal pattern and the small standard deviations. The error bars are standard errors of the all-tree means averaged over the nine days centered on the presented Day of Year.

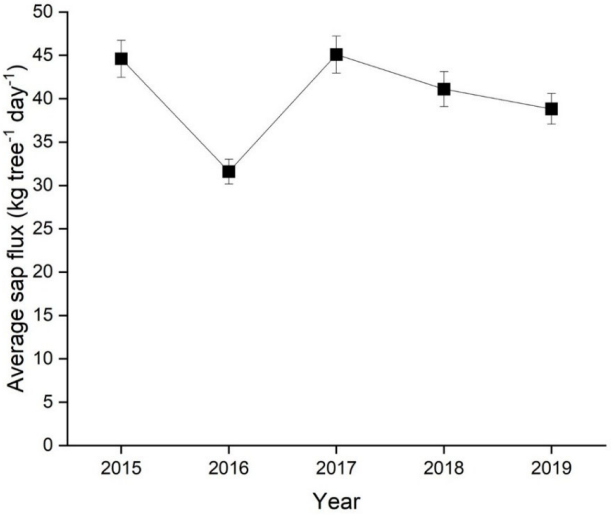

Fig. 3. Average sap flux per tree per day, estimated from gap-filled data for DOY 91-304. Standard error bars are shown.

3.3 Isotopes and Water-use efficiency

The years differed in stable isotope composition (Table S1) and intrinsic water-use efficiency. The year 2018, which is widely recognized as an extreme drought year in large parts of Europe (Bastos et al., 2020), stands out for its low discrimination (Fig. 4).

https://doi.org/10.5194/egusphere-2026-5424
Preprint. Discussion started: 16 September 2026

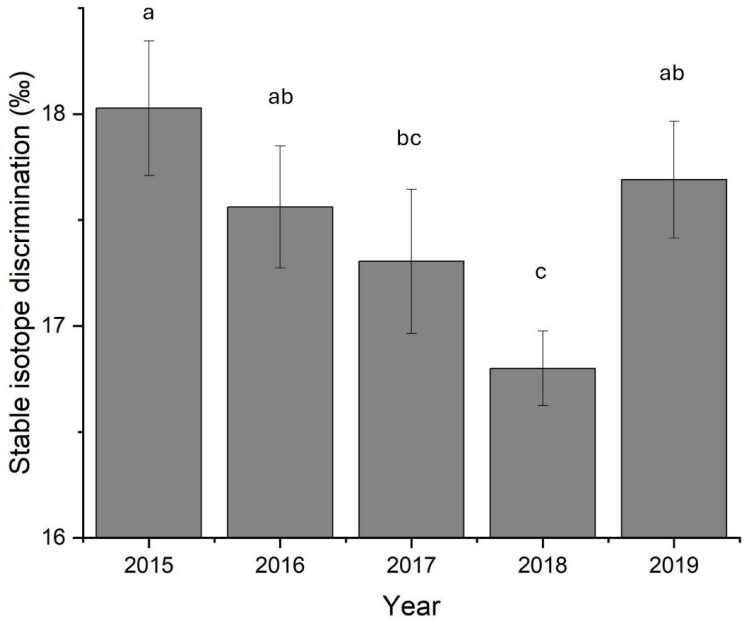

Fig. 4. Stable carbon isotope (^{13}C) discrimination (Δ) of annual rings of sap-flux trees by year. Δ is inversely related to intrinsic water-use efficiency (iWUE). Error bars show standard errors and different letters signify differences among the years in Tukey's HSD at α = 0.05.

3.4 Eddy covariance (NEE and GPP)

The daily GPP estimates from EC are compared to estimates from isotopes and sapflux (IsoSF), and nine-day averages of IsoSF (Fig. 5). There was a general pattern of agreement between methods, with several exceptions. In particular, the spring of 2015 had higher IsoSF than EC estimates. After about day 180 of that year, the two methods agreed better. The agreement was good throughout the whole of 2016. There were several data gaps in 2017 (shown as gray bars), but agreement was otherwise good. In 2018, a year of severe summer drought, there was a strong reduction in GPP detected by both methods during the drought period. In 2019, which included data from almost the complete annual cycle, the spring difference between methods again appeared around the time sap flux began (Fig. 5).

Focusing on the severe drought of summer 2018, we detected a decline in GPP by both methods, but it was more pronounced in IsoSF results (Fig. 6). We compared the 2018 data to the means for the other years between days 171 and 222, which comprised the drought period in 2018. We found that the EC method estimated a loss of approximately 90 g C m^{-2} (Fig. 6a), or about 13% of the normal total for these days. In contrast, the IsoSF data estimated a loss of 253 g C m^{-2} (Fig. 6b), or 31%. Moreover, the IsoSF data show a consistent decline in GPP that seems more physiologically credible than the variation in the EC data. It is also useful to compare the timing of the responses to the timing of the rain-free period (Fig. S3). The decline in IsoSF GPP data shows a steady decline during the period without precipitation. It partially recovered when the rains returned but continued below the long-term mean for several weeks thereafter (Fig. 6b).

https://doi.org/10.5194/egusphere-2026-5424
Preprint. Discussion started: 16 September 2026

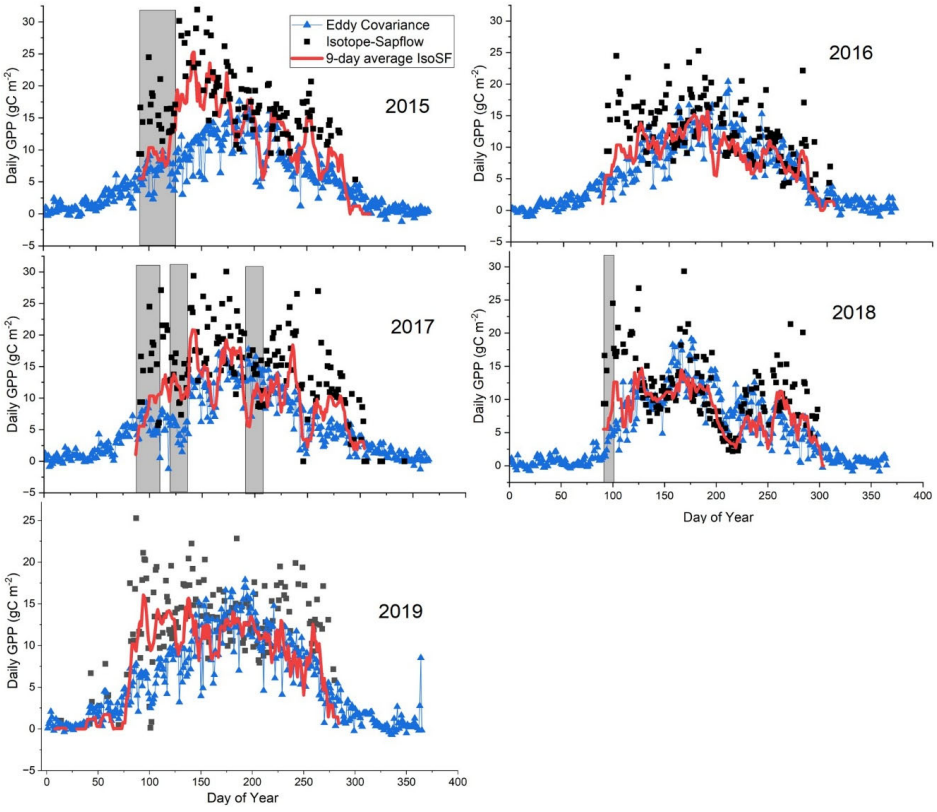

Fig. 5. Daily estimates of GPP from eddy covariance (blue line), stable isotopes and sap flux (IsoSF; black squares), and nine-day averages of IsoSF (heavy red line) at Central forest, Skogaryd Research Catchment. The gray boxes show periods for which IsoSF was gap-filled.

210

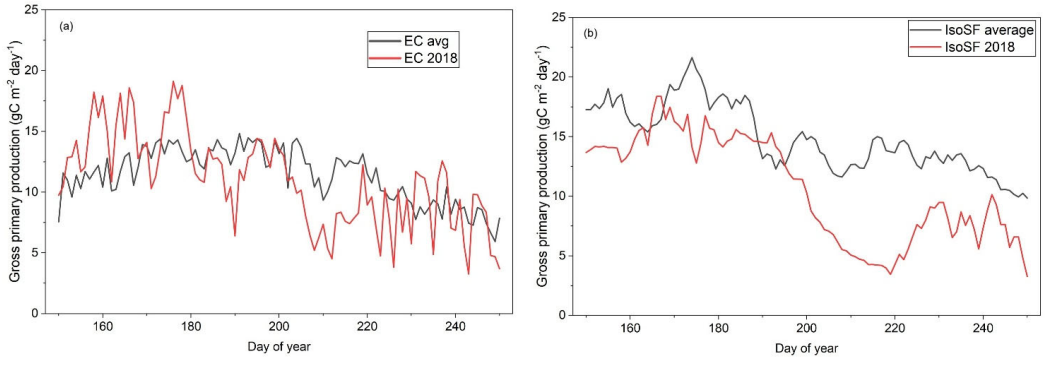

Figure 6. Daily gross primary production at the Central forest, Skogaryd Research Catchment estimated from (a) eddy covariance (EC) and (b) isotopes and sap flux (IsoSF), where the black lines represent the means of 2015, 2016, 2017, and 2019 and the red lines represent 2018. The drought of 2018 began on day 177 and lasted until day 222. The gap between the lines represents the GPP lost due to the drought in 2018.

215

https://doi.org/10.5194/egusphere-2026-5424
Preprint. Discussion started: 16 September 2026

The GPP sums for the period Apr 1 to Oct 31 were compared between methods (Fig. 7). The IsoSF method yielded higher GPP sums during the years when IsoSF yielded higher GPP estimates in the spring, especially 2015, but the summed GPP values were similar in 2016 and 2018. Annual sums by EC were 2017, 2070, 2016, 1931, and 2170 g C m^{-2} yr^{-1} in the years 2015-2019. The period from Apr 1 to Oct 31 included 92 (SE=2)% of the annual GPP sum as measured by EC.

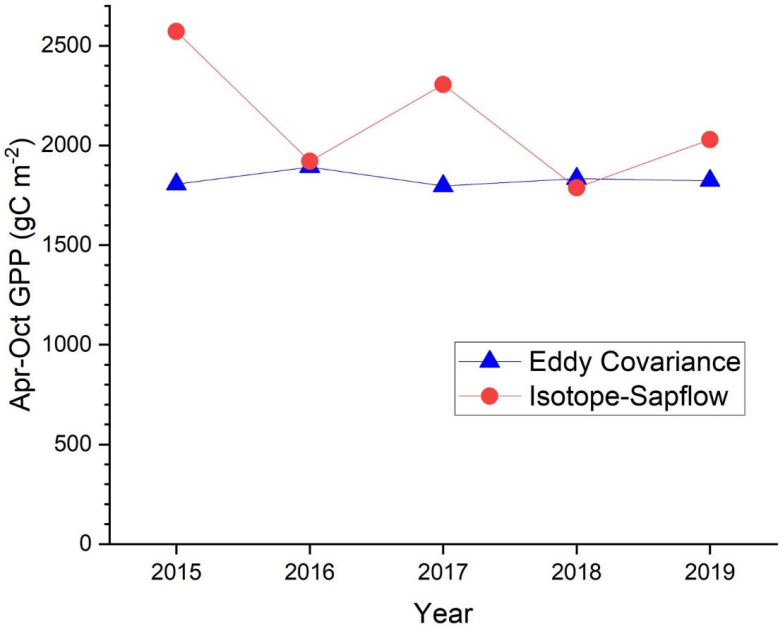

Fig. 7. Gross primary production summed for the period 1 April to 31 October based on eddy covariance estimates and isotope-sapflow estimates at Central Forest, Skogaryd Research Catchment.

4 Discussion

We compared two independent means of estimating GPP across five years in a rapid-growing spruce plantation. We found frequent agreement in daily GPP values, with occasional exceptions in mid-spring. The IsoSF method described much clearer and consistent reductions in GPP than the EC method during the drought of 2018. This paper is among the first to perform such analysis with the isotopic composition of whole annual tree rings, making it possible to estimate GPP by this method wherever sap-flux has been measured.

4.1 Biomass and Productivity

The forest at Skogaryd provides an important reference point because it is among the most productive in Sweden, presumably due to fertile, nutrient-rich soil and the ditching, favoring nutrient mineralization (He et al., 2016). The height growth at the site (up-to 32 m at 60 years, Fig. 1) is above the highest range reported for Swedish spruce forests (Mensah et al., 2022). In terms of C budgets, on a nearby spruce plantation on drained organic soil, NPP was 830 g C m^{-2} yr^{-1} (Meyer et al., 2013) and He et al. (2016) estimated whole-tree biomass production, which stabilized (~800 g C m^{-2} yr^{-1}) when the stand reached 20 years of age. Aurangojeb et al. (2017) reported even higher productivity for the Central forest, where the present study was conducted (1020 ± 33 g C m^{-2} yr^{-1}).

https://doi.org/10.5194/egusphere-2026-5424
Preprint. Discussion started: 16 September 2026

4.2 Eddy covariance

Eddy covariance data have been presented for forests at the Skogaryd Research Catchment several times before. Meyer et al. (2013) compared NEE of a spruce plantation on drained organic soil to estimates based on component fluxes and concluded that considerations of error structure favored the EC estimates. This comparison occurred before a series of papers raising questions about canopy decoupling in densely forested systems (Thomas et al., 2013; Jocher et al., 2018), which might challenge that conclusion. A second paper compared the Central forest to other Nordic forests during 2018, a year of severe summer drought (Lindroth et al., 2020). Lindroth et al. (2020) highlighted the strong effect of drought on annual NEP at Skogaryd but attributed it exclusively to a change in ecosystem respiration. Uniquely among the eleven Nordic sites, the drought effect on GPP was effectively zero. Here we present the daily EC estimates of GPP in 2018 (Fig. 6a) and show that there was in fact a reduction in GPP during the drought, which was presumably obscured in the annual sums reported on earlier. Finally, our site was included in a model comparison (Junttila et al., 2023). Although Skogaryd was not explicitly discussed in this paper, model performance during the drought of 2018 was addressed.

Our EC based estimates of GPP were derived using the nighttime flux partitioning method (Reichstein et al., 2005), which relies on the temperature response function of nighttime NEE, which equals ecosystem respiration, and assume the same response functions for ecosystem respiration during daytime. However, the partitioning by this method was inconsistent with a stable isotope partitioning (Oikawa et al., 2017), where the latter resulted in 10-13 % lower GPP estimates compared to the nighttime approach. This contrasts with our IsoSF based GPP estimates, which were equal to or tended to be higher than the EC based GPP (Fig. 7). More fundamentally, the EC method can have difficulty with conditions that decouple the air masses above and below the canopy, possibly leading to advection of respired CO_2 to or from the study site (Thomas et al., 2013; Jocher et al., 2018, 2020). Unless such events are filtered out, they influence NEP estimates in a way that would likely be carried over into inferences of GPP. Our site was flat, but the canopy was dense. No rigorous measurements of decoupling have yet been conducted there, adding unknown uncertainty to the GPP inferences by this method.

4.3 Isotopes/Sap flux

The tree-ring stable isotope data, expressed as discrimination against ^{13}C of atmospheric CO_2, varied distinctly among years. We observed higher water-use efficiency in the dry years, as expected. The one year of complete sap flux data, 2019, showed a rise above zero around day 70 and declined to near zero again around day 270 (Fig. 2), which coincided roughly in time with the rise of GPP based on EC, as expected. High rates of sap-flux were observed in the spring of 2015, which contributed to high GPP_{IsoSF} during that period, considerably higher than estimates from EC. We are unable to explain these high values, but we speculate that there may have been sap-flux uncoupled from photosynthesis during that period, perhaps associated with freezing and thawing events (Charrier et al., 2017). If so, it would likely lead to false inference of ongoing photosynthesis. In some of our earlier work using IsoSF techniques (Vernay et al., 2020, 2024), we used a temperature-based algorithm to filter out periods when photosynthesis was unlikely to have begun. Such a filter might have removed these results as well.

In summer of 2018, the drought-induced reduction was less severe in the GPP estimates from EC than in those from the IsoSF (Fig. 6). The relatively high VPD during this period tended to improve the IsoSF estimates of canopy conductance, increasing our confidence in these estimates. Average sap flux during the drought fell from 94 kg $tree^{-1}$ day^{-1} to less than 10 kg $tree^{-1}$ day^{-1}. Because the stable isotope composition was measured across the whole annual tree-ring, the isotopic data might have failed to detect an increase in isotopic composition during the drought, as observed elsewhere (Schiestl-Aalto et al., 2021). However, the observed ten-fold reduction of sap-flux would require a ten-fold increase of intrinsic water-use efficiency to compensate; such an increase in iWUE is unlikely in a conifer forest (e.g., Vernay et al., 2020).

4.4 GPP methods comparison

https://doi.org/10.5194/egusphere-2026-5424
Preprint. Discussion started: 16 September 2026

The annual sums of GPP are broadly comparable between the two methods throughout the study period (Fig. 7). Recall that the nine-day averages, shown as heavy red lines in Fig. 5, include days with zero GPP, which resulted from the VPD filter (<0.002 hPa). However, the IsoSF estimates were substantially higher than the EC estimates, especially in 2015. As noted above, the EC data have been questioned with respect to decoupling of above- vs. below-canopy fluxes (Thomas et al., 2013; Jocher et al., 2018), especially in the presence of dense canopies such as the spruce forest studied here. Although we did not explicitly measure canopy decoupling, vertical temperature profiles tended to support the notion that decoupling occurred, especially at night. If so, the inference of GPP might be influenced by advective interference, especially in the night-time flux estimates (Thomas et al., 2013; Jocher et al., 2018).

The IsoSF estimates of GPP have room for error as well. In particular, the high estimates of daily GPP in the spring of 2015 may have been influenced by the low VPD in that year. Because canopy conductance is estimated by dividing sap flux by VPD, a near-zero VPD could yield poorly constrained results. We addressed this problem by filtering out days with VPD < 0.002 hPa (Vernay et al., 2020, 2024), but even this filtering may have allowed for unrealistic estimates at the lowest VPD values. Moreover, this approach assumes that there is negligible GPP on days with low VPD_d, which is not what we see in the GPP_{EC} data. In any case, the methods agree well when VPD is high, as in the middle of the growing season. Another potential source of error is that the isotopic composition of photosynthate can change along the length of the stem, which would interfere with inferences of canopy gas-exchange (Gessler et al., 2009; Offermann et al., 2011). We have neglected such potential changes in the current manuscript based on previous successful applications of this approach (Ubierna & Marshall, 2011; Vernay et al., 2020; Gimeno et al., 2021).

To summarize this comparison, it seems unlikely that the daily GPP values in the spring of 2015 were as high as the IsoSF method predicted (Fig. 5), leading to upwardly biased annual GPP estimates during that time. Seasonal discrepancies between IsoSF estimates and EC have been observed before (Vernay et al., 2020, 2024; Stojanović et al., 2024), but they have occurred in late summer and early fall, not in the spring as they did here. The problems may have been worsened by sampling the isotopic composition of the whole tree ring. The agreement between the methods in the rest of the year, however, leads us to believe that the two methods are in general measuring similar fluxes. The clearest exception is during the severe drought of 2018, when the low sap-flux estimates led to credibly lower GPP estimates by the IsoSF method.

4.5 Stem wood production efficiency

We estimated the efficiency of mean stemwood production relative to GPP over the whole stand and the whole period. Our estimate of aboveground stem production alone (237 g C m^{-2} yr^{-1}) relies on fewer assumptions about litterfall and root turnover than previous estimates of total NPP at the site (e.g., Aurangojeb et al., 2017). These stem data support the conclusion that this forest is exceptionally productive by Swedish standards. An important simplification was that understory biomass was so negligible in relation to tree biomass (He et al., 2016), that it could be neglected in parameterization of the C budget. The resulting efficiency was 17%, which is higher than the 11% for a reference pine stand and 15% in an intensively fertilized pine stand in northern Sweden (Marshall et al., 2023), but it is similar to an estimate of 16 (SD=4)% for spruce in the Czech Republic (Krejza et al., 2022). This value supports our methods and measurements, while also suggesting that the forest at Skogaryd has high partitioning to stem production, perhaps helping to explain its rapid growth.

The estimates of iWUE used in this study were derived from the isotopic discrimination against ^{13}C in complete annual tree rings. This whole-ring approach, which has been used before (Klein et al., 2016), has the advantage of integrating across the whole growing season, supporting conclusions about annual sums. Its disadvantage is that it misses short-term events such as the drought of 2018. There may be value in short-term isotopic data based on phloem contents (e.g., Vernay et al., 2020) or laser-ablation across tree rings (Saurer et al., 2023; Marshall, 2023) in future studies of drought effects.

https://doi.org/10.5194/egusphere-2026-5424
Preprint. Discussion started: 16 September 2026

Data availability

Eddy covariance and sap-flux data will be made available on acceptance of the paper in the European Fluxes Database Cluster (www.europe-fluxdata.eu/home/site-details?id=SE-Sgr) and the SITES data portal (https://data.fieldsites.se/portal/), respectively. The tree ring isotope are available in Table S1.

Author contributions

Tobias Rütting: Conceptualization, Data curation, Formal analysis, Funding acquisition, Writing – original draft; Maj-Lena Finnander Linderson: Data curation, Writing – review and editing; Per Weslien: Data curation, Writing – review and editing; Lasse Tarvainen: Writing – review and editing; John D. Marshall: Conceptualization, Data curation, Formal analysis, Funding acquisition, Writing – original draft.

Competing interests

The authors declare no competing interests

Acknowledgements

We are grateful to David Allbrand, Bengt Liljebladh, Mauricio Fuentes, Josefina Carlberg and Andreas Arleborg for support in the field and laboratory.

This paper is a contribution to the Strategic Research Area "Biodiversity and Ecosystem Services in a Changing Climate" (BECC) funded by the Swedish government. We acknowledge the Swedish Infrastructure for Ecosystem Science (SITES), funded by the Swedish Research Council (VR), for maintaining the Skogaryd Research Catchment.

Financial support

The work has been supported by FORMAS – Swedish Research Council for Sustainable Development (2022-00891).

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